great, indeed, in no essential are they different, except that the former usually goes forward in a bilaterally symmetrical way, while in the latter it most frequently does not.

The preceding facts and considerations embrace what may be regarded as the complementary principle demonstrating the mechanical theory of axial segmentation or origin of vertebræ, as proposed by Spencer, since it must be allowed, that if segmentation is due to flexures of the vertebral axis, conversely, union, coössification of segments, is due to their absence, because opposite conditioning causes must produce opposite effects in two things respectively so conditioned.

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ON THE TRANSPIRATION OF PLANTS.[1]

BY J. M. ANDERS, M.D., PH.D.

IN looking over the literature of the subject, one is surprised to find how little definite knowledge we possess in regard to the process of plant transpiration. When the importance of the subject is considered, there would seem to be no explanation for this apparent omission of research.

It has been pretty well established that transpiration is produced and modified by influences acting from without, and by the structural peculiarities of the plant. Most important among the former modifying agencies are sunlight, wind, dew point and temperature ; and among the latter circumstances is to be mentioned, more particularly, the nature of the epidermal tissue. The precise connection between these various conditions and the amount of water evaporated has not been investigated to any considerable extent; and the most important question, viz.: the amount of liquid ordinarily transpired by different plants has, also, hitherto been quite as sadly neglected.

A few bare statements are made in relation to the quantity of transpiration (Gray's Structural and Systematic Botany). A sunflower 3½ feet high, with a leaf surface of 5616 square inches, when exposed to the air, evaporated from 20 to 30 ounces in twelve hours, being seventeen times as fast as man exhales. A seedling apple tree, with leaf surface amounting to 112 square feet, evapo-

[1] The Geo. B. Wood prize essay, 1877, read before the Society of the Alumni of the Auxiliary Dept of Medicine, University of Pennsylvania.

rated at the rate of 9 ounces per diem, and a vine with twelve square feet of leaf surface, transpired at the rate of 5 to 6 ounces per day. The sunflower during a dry night lost 3 ounces, but nothing on a dewy night. The method adopted in these experiments is not referred to by him.

Balfour, in his work on botany (page 457), refers to the investigations of Woodward, giving some of the results of this observer. Woodward took plants, and, having immersed their roots in water, placed them in the light for more than a month. He noticed the quantity of water absorbed and the amount transpired (making allowance for extraneous evaporation), and showed that the greater quantity of the water absorbed was again given off by the leaves.

It is questionable whether results thus obtained are to be relied upon, inasmuch as these plants must have been placed under unnatural conditions and influences, by allowing their roots to rest in pure water; for it is a known fact that certain plants (Calla Æthiopica, for instance) can be made to distill the water in drops from their leaves, if too abundantly supplied to their roots.

Curiously enough, in every instance in which the methods adopted have been detailed, the objectionable circumstance of placing the plants in a very unnatural state while experimenting upon them has obtained. Reference is here made only to experiments on entire plants. The results of the observations of Garreau (Annales des Sciences Nat. 3d Ser. Bot. xiii. 355) on the transpiration from leaves should, doubtless, be accepted as reliable, if we consider the means employed. This observer estimated the amount of exhalation by collecting it by means of chloride of calcium, placing the leaf between two bell-jars, one applied to its upper and the other to its under surface. His conclusions were:

"1. The quantity of water exhaled by the upper and under surfaces of the leaves is usually as 1 to 2, 1 to 3, or even 1 to 5 or more. The quantity has no relation to the position of the surfaces, for the leaves when reversed gave the same results as when in their natural position. 2. There is a correspondence between the quantity of water exhaled and the number of stomata. 3. The transpiration of fluid takes place in greater quantity on the parts of the epidermis where there is least waxy or fatty matter as along the line of the ribs."

Among the reported results that my eye has been able to reach, the foregoing only are considered worthy of special notice. Possibly some have escaped notice.

The present experiments have been performed more especially with the view of ascertaining, as nearly as possible, the amount of water evaporated by plants in a healthy, natural state, and, also, to determine the connection between the meteorological conditions and variations and the nature of the cortical tissue, and transpiration. The importance of keeping the plants in a perfectly normal state while being experimented upon was called attention to by Prof. Rothrock when lecturing on the subject of evaporation from plants. To accomplish this it was suggested by him at the time that something impervious to moisture be adjusted to the receptacle in which the plant had previously been growing, fitting the same accurately to the base of the stem, the object of it all being to prevent any evaporation from the vessel or earth in which the plant was situated, so that all evaporation would be from the plant itself above the ground. The plant was now to be weighed at stated intervals and the loss of weight in any given time would represent the weight of the liquid transpired. It is evident that this, with properly balanced scales, would show exactly the quantity evaporated, save the slight increase in weight of the plant by the gases derived from the air which it fixes in the time of one experiment. This certainly must be regarded as extremely small when we reflect that plants return to the atmosphere the greater portion by volume of the gases absorbed by them. The circumstance of plants gaining slightly in the course of a day by the gases they fix from the air, it will be observed, is not calculated to favor an over-estimate of the quantity transpired.

The means employed to accomplish these ends were as follows:

A piece of good rubber cloth of sufficient size was taken and its narrower border tucked up neatly around the base of the stem of the plant and secured by means of an elastic cord. The rubber cloth was then allowed to drop down over the vessel in which the plant was situated, the portion of the cloth underneath the pot gathered up and brought to one side of its base, and after giving it a few twists in one direction so as to insure its close application to all parts of the pot, the twisted portion was well wrapped and tied off by means of a cord so as to keep it in this condition. This

done, the line of separation at the point where the edges of the cloth met, was remedied by allowing an overlapping of two inches or more and sealing by means of gum mucilage. It was now thought that evaporation from the vessel in which the plant was situated was next to impossible; but the question next arose, "How is the plant to be supplied with the necessary moisture?" This difficulty was overcome by taking a hollow cylinder of tin 3-4 inch in diameter, and about 3 inches in length, and having made a hole of sufficient size in the cloth covering the pot, a few inches from the stem of the plant, introducing one end of this tube into the opening, the rubber cloth was tucked up and tied on it the same as in the case of the stem of the plant, the external opening of the tube being guarded by means of a cork.

It would be useless, as well as illogical to assert that this arrangement would allow of no escape of moisture whatever, yet there is perfect safety in affirming that the quantity thus lost sinks into insignificance compared with the amount actually transpired by the plant itself. The loss by insecurity of this method could certainly not exceed a few grains per day.

The plants were watered in the morning before weighing them for the day's experiment, and just sufficient water was given them to keep them in a natural state, the condition of the leaves being in all cases taken as a guide. After watering the plants in the morning they were carefully weighed and then placed in the desired position and left undisturbed till evening, or any number of hours desirable, and then were again weighed (as a rule before any more water was given). The loss of weight, as before stated, was considered equivalent to the amount evaporated during the time of the experiments.

Usually the observations were made for a day and a night, but the plants were also weighed in the evening so as to establish the relation between night and day evaporation during the same twenty-four hours. As before intimated the relationship between the dew point, temperature, etc., and the rapidity of transpiration was noted in most of the observations made. This was arrived at by means of the ordinary wet bulb thermometer, taking the average temperature and dew point according to the well known rule, which it would be needless to detail here.

With this brief yet, it is hoped, sufficiently comprehensible description of methods pursued, we shall pass to the notice of results obtained by these researches.

Plant No. 1 employed, was a common Calla (*Calla Æthiopica*), an herbaceous plant 3 feet 1½ inches high. Its whole weight on taking it up, with roots cleaned, was 2 pounds 2 ounces; weight of evaporating portion, or all above ground, 1 pound 3 ounces, 240 grains in a green state; complete weight of outfit, including plant, vessel, and apparatus adjusted for experimentation, 21 pounds 4 ounces 20 grains. This latter weight is here stated in order to avoid an unnecessary record of figures in the table of results to follow, by giving the weight of the growing plant at each time it was taken. Suffice it to give the loss of weight, or its equivalent the amount of water evaporated during the periods of time indicated. The same plan will be pursued hereafter.

The following are the results with this plant:

Ex.	Duration of Experiment.	Loss of weight or amount evaporated.	Place.	Weather.
I	12 hours, day.	1420 gr.	Indoors.	Clear.
II	12 "	195 "	"	Cloudy, rain.
III	12 "	1440 "	"	Clear and warm.
IV	12 "	2040 "	In open air.	Partly cloudy.
V	12 "	2380 "	"	Clear,
VI	12 "	3320 "	"	Clear, windy.

The important part played by the sun's rays and atmospheric currents in transpiration is very well shown by these results. The plant while indoors received the sun's rays only about half the time during a clear day, which was the case in all indoor experiments made, and, although the room in which it was kept was well ventilated, the currents were in no way comparable to the circulation of the atmosphere outside. It was found, very curiously, that this plant evaporated nothing during a cloudy night in or out of doors, and only about 460 grains on an average during clear nights in open air.

Plant No. 2 was one of our common geraniums (*Pelargonium cucullata*); also herbaceous; 18 inches high; weight in a green state, with roots washed, 9 ounces 120 grains; of green or exhaling part 7 ounces; complete weight fitted for experimentation, 9 pounds 15 ounces 350 grains. The evaporating surface of the two first plants tried was not estimated on account of the shape of the leaves, and the extent of the branches in the case of the geranium and of the leaf stalks in the case of the calla (which it would have been necessary to include) rendering it too difficult for the observer. It might be well to state here that the plants

were taken up *after* the experiments made upon them, in order to ascertain their weight.

The geranium gave the following results :

Ex.	Duration of experiment.	Loss by evaporation.	Loss by day, 12 hours.	Place.	Weather.
I	Day and night.	1560 gr.	1080 gr.	Indoors.	Clear.
II	"	1930 "	1440 "	"	Clear, warm.
III	——	——	1286 "	"	Clear.
IV	Day and night.	3380 "	2880 "	In open air.	Clear.
V	"	3730 "	3220 "	"	Clear, very warm.
VI	"	3390 "	2900 "	"	Clear.

These results indicate that the amount exhaled at night is about the same in the open air as in the house, while the evaporation in day time is more than double in the former position what it is in the latter in the same length of time. It will be observed that this plant evaporated more than the weight of the portion with exhaling surface in the course of twenty-four hours. It should be remarked that this and the previous plant were in the flowering stage.

Plant No. 3, a fuchsia (*F. macrostemma*), was a shrubby plant in the flowering stage; leaf surface estimated at 450 square inches; height of plant 27 inches; weight of the portion having evaporating surface 2 ounces; of whole plant, with roots washed and in a green state, 4 ounces; complete weight of outfit ready for experiment, 9 pounds 15 ounces 360 grains.

Coincident with the remainder of the experiments, daily observations were also made on the average temperature and dew point. It should be stated that these latter observations were taken in the same medium in which the plant was situated.

This plant gave the following interesting results:

	Duration of Experiment.	Loss of weight by evapora'n	Loss by day, 12 hours.	Avera'e temperature.	Average dew point.	Place.	Weather.
I	Day and night	1810 gr.	1260 gr.	77.°	61.4°	Indoors.	Clear.
II	"	1800 "	1240 "	72.	51.2	"	Clear.
III	"	1450 "	980 "	68.	49.9	"	Partly cloudy.
IV	"	2270 "	1910 "	63.5	49.5	In open air	Cloudy, some rain.
V	"	2415 "	1930 "	65.9	50.5	"	Clear, partly cloudy.
VI	"	2510 "	2020 "	65.	49.9	"	Clear, windy.

It will have been observed that the average temperature was higher, and the dew point consequently correspondingly lower during the time of the observations made on this plant in the

house than when exposed to the open air; this, no doubt, accounts for the fact that more was lost at night while indoors than when exposed, as may be seen by subtracting the amounts evaporated by day, in the table, from the whole amounts given off in twenty-four hours, the *average* at night having been 540 grains per night while indoors, and only 422 grains per night outside. Temperature and the relative humidity of the atmosphere would therefore seem to influence transpiration at night, the weather, apart from the conditions mentioned, having been about the same at night in the two cases. These results also show that the process is at least twice as active when the plant is exposed during the day as when kept in the house; and yet, as before intimated, the average temperature and the complement of the dew point were higher during the experiments made indoors than when the plant was out of doors. This would go to show that sunlight and currents of air are, one or both of them, great modifiers of this process.

It is interesting to notice that this plant evaporated 100 grains more than its own weight (4 ounces) in twelve hours.

Plant No. 4, *Hydrangea arborescens*, a shrubby plant in æstivating stage, 2 feet high; weighed, in a green state with roots cleaned, 4 ounces 250 grains; leaves alone, 2 ounces 250 grains; evaporating surface of leaves, 744 square inches; complete weight of plant fitted for experimentation, 7 pounds 11 ounces 240 grains.

It was found on taking up this plant, after the experiments had been made on it, that the quantity of earth its roots had to draw moisture from was rather too small, notwithstanding this circumstance, however, the results obtained are full of interest. They are the following:

Ex.	Place of experiment.	Duration of experiment.	Loss of weight by evapora'n	Loss by day, 12 hours.	Avera'e temperature.	Average dew point.	Weather.
I	In open air	Day and night	3010 gr.	2450 gr.	71.°	54.6°	Clear, windy.
II	"	"	2395 "	1910 "	71.	55.8	Clear, calm.
III	"	"	2425 "	1940 "	75.5	59.2	Clear.
IV	"	"	2515 "	2045 "	75.	57.5	Clear.
V	Indoors.	"	1460 "	975 "	79.	58.7	Clear.
VI	"	"	1370 "	900 "	80.	59.8	Clear.

In proportion to the extent of evaporating surface, this plant did not exhale as much as the Fuchsia; whereas the relation between the weights of the two plants, and the quantity evaporated by each respectively, is about the same. In the case of the

Fuchsia strong currents of air hastened the process, for while on the last day the Fuchsia was experimented with, the temperature was no higher and the difference between the dry bulb and dew point was not as great as on the previous day, it was found to exhale most—exceeding all the rest of the results by 92 grains. This latter excess, under the circumstances, must, in part at least, have been due to atmospheric currents, which were more prevalent on that day. The influence of these currents was still better exemplified by the results from the Hydrangea. It will have been noticed that this plant evaporated, at least an ounce more during experiment I. than on any succeeding day. The atmospheric currents no doubt produce their effect in a mechanical manner. They remove vaporized fluid as it is formed, and thus really act as a *vis a fronte* to the vaporizing liquid within.

Apart from the influence of winds, and given a clear day, a glance at the two last tables of results will show a direct correspondence between the complement of the dew point and the rate of transpiration in these cases. This latter fact will become more evident hereafter.

A few observations were made on the Hydrangea with the view of determining the rate of evaporation of different periods during the day. It was found that this plant while in the open air evaporated between the hours of 11 A. M. and 3 P. M. as much as in the remaining eight hours of the day's experiment.

Plant No. 5 was a *Camellia japonica*, a shrubby plant 28 inches high; leaf surface 479 square inches; complete weight of outfit ready for experiment, 8 pounds 12 ounces 40 grains.

The following results were obtained:

Ex.	Duration of experiment.	Loss of weight by evapora'n	Loss by day, 12 hours.	Av'ge temperature.	Av'ge dew point.	Place of experiment.	Weather.
I	Day and night	710 gr.	710 gr.	78.5°	63.3°	In open air	Clear.
II	"	650 "	650 "	79.5	71.3	"	Cloudy part, some rain.
III	"	170 "	480 "	70.	61.5	"	Cloudy, clear at night
IV	"		240 "	74.	63.	Indoors.	Cloudy.
V	"	10 "	190 "	74.	65.7	"	Cloudy and rainy in part.
VI	"	250 "	250 "	74.5	65.8	"	Clear.

These results exhibit in a satisfactory manner the connection between the character of the leaf structure and the rapidity of evaporation. The fact that this plant had leaves of dense structure and with thick cortical coverings must account for the very much smaller quantity of evaporation; and yet some allowance

ought to be made in this case for the less favorable meterological conditions during the time this plant was used, as shown by the table.

Again, it is very probable that in plants with evergreen leaves having thick epidermal tissue evaporation is only possible through the stomata, whereas in the case of leaves which are thin, soft and rapidly growing, with little cortical tissue, evaporation is more general from their surfaces. It is quite possible, also, that the number of stomata in the case of the Camellia is below the average. However these things may be, the fact remains, that the nature of the cuticular tissue of the leaves is hereby shown to be closely related to the amount of liquid transpired.

This plant exposed during a cloudy and dewy night gained in weight to the extent of 310 gr., as shown by the table; the same thing occurred on a rainy night in the house, when the plant was situated about four feet from an open window, as was the case in all indoor experiments; the gain in the latter case, as shown by the table, being 230 gr. There was no loss by evaporation at night in the open air.

Plant No. 6, was a Lantana (*L. carnosa*), a shrubby plant, 18 inches high; leaf surface 330 square inches; weight only 1½ ounces; complete weight fitted for experimentation, 5 pounds 2 ounces 250 grains.

The following are the results:

Ex.	Duration of Experiment.	Loss by Evaporation.	Loss by day, 12 hours.	Av'ge temperature.	Av'ge dew point	Place.	Weather.
I	Day nd night	1360 gr.	1200 gr.	66.°	52.2°	In open air	Clear, cloudy.
II	"	988 "	688 "	64.	54.4	"	Cloudy during day.
III	"	1820 "	1820 "	76.	63.3	"	Cl'r, windy dewy n't.
IV	"	2120 "	1920 "	79.5	65.6	"	Clear, windy day.
V	....	....	1930 "	79.	66.	"	Clear, windy.

The leaves of this little plant were very thin and soft, which may account, in a measure at least, for the great rapidity of transpiration from their surfaces. As compared to the extent of leaf surface, this plant evaporated more than any other plants tried, reaching, in a clear windy day, nearly 2 ounces per square foot of leaf surface in twelve hours. It will be observed that the Lantana evaporated nearly three times its own weight in twelve hours.

A few experiments were made with this plant (as was done with the Hydrangea) to ascertain how much more rapid the process was about midday than at other periods of the day. It was found

to be most rapid about noon and a little after; and it was found here, also, that half the quantity evaporated by day was given off between the hours of 11 A. M. and 3 P. M. These observations were made on clear days.

The last, or plant No. 7, was a Dracæna, an herbaceous plant with large leaves (being cultivated for its foliage). Its leaf surface was estimated at 817 square inches; its height 27 inches; weight not taken; complete weight of outfit, 11 pounds 6 ounces.

The following are the results obtained:

Ex.	Duration of experiment.	Loss of weight by evaporatn	Loss by day, 12 hours.	Aver'ge temperature.	Average dew point.	Place.	Weather.
I	Day and night	2784 gr.	2410 gr.	66°	52.2°	In open air	Clear.
II	"	1870 "	1385 "	64.	54.4	"	Cloudy, clear at night.
III	"	2601 "	2351 "	76.	63.3	"	Clear, during night.
IV	"	2670 "	2410 "	79.5	66.6	"	Clear, windy day, do.
V	"	2770 "	2520 "	79.	66.	"	Clear, much wind.

In comparison to the extent of leaf surface, this plant did not transpire as fast as most of the other plants used. The fact of the Dracæna having smooth and more or less hard leaves, no doubt accounts for the relatively less rapid evaporation from its surface. In the case of the two last plants tried, it may have been noticed, as in the two before them, that, other things being equal, dryness of the atmosphere was favorable to the process of transpiration.

In experiments IV and V, with both the Lantana and Dracæna, are shown once more the favorable influence of winds over this process in plants. The scales used in all these experiments were accurately adjusted.

Summary of Investigations.

In clear weather the evaporation by night as compared to that which takes place in the day appears to be about in the ratio of 1 to 5. In some cases no loss occurred on dewy or cloudy nights. The Camellia, however, lost nothing during clear nights, and gained in weight on dewy or rainy nights, even when kept indoors. Under ordinary circumstances evaporation at night was about the same indoors as in the open air.

The rate of transpiration during the day showed a very different relation, giving a ratio of 2 to 1 in favor of the open air. Of the whole amount evaporated during twelve hours, in the day experiments, half was given off between the hours of 11 A. M. and 3 P. M., as shown by repeated testing.

The following table, compiled for the number of clear days, will serve to exhibit the average rate of transpiration by day which took place in the open air during clear weather. It will also indicate the relation between leaf surface and the weight of the plant, and amount transpired.

The mean temperature and average dew point have also been recorded in the table.

No.	Name of Plant.	Duration of experiments	Average evaporati'n	Evaporating surface.	Weight of plant.	Average temp'ture.	Average dew point.
1	Calla........	12 hours.	2850 gr.	All parts green	2 lb. 2 oz.	....	....
2	Geranium....	"	3500 "	....	4420 gr.	....	....
3	Fuchsia.....	"	1975 "	450 sq. in.	1920 "	64.5°	49.6°
4	Hydrangea..	"	2858 "	744 "	2170 "	73.	56.7
5	Camellia....	"	710 "	479 "	....	75.5	63.3
6	Lantana.....	"	1717½ "	330 "	720 "	75.1	61.7
7	Dracæna....	"	2422 "	817 "	....	75.5	62.

After an inspection of this table, the average rate of evaporation for soft, thin-leaved plants, in clear weather, may be put down at about 1¼ ounces per day (12 hours) for every square foot of leaf surface. The Lantana shows nearly 2 ounces to the square foot of surface. The Camellia, with its dense, smooth leaves, averaged less than half an ounce to the square foot of surface, per day.

The nature of the leaf structure modifies very greatly the rate of evaporation, as may be seen by comparing the results from the Camellia with those of other plants having soft and thin leaves.

Apart from structural peculiarities, no doubt the sun's rays stand first in importance among the modifying influences; for going back to the results from the Fuchsia, for instance, we find the average temperature higher and the dew point greater during the indoor experiments than when the plant was exposed, and yet the relation of evaporation in the two situations was, other things being equal, about as ordinarily the case. The same obtained in the case of the Hydrangea in a still more marked degree.

It is still an unsettled question whether radiation, as such, produces this great effect, or whether it is through the heat that accompanies the rays, or the chemical changes they produce.

That the difference between indoor and out of door evaporation was not due so much to atmospheric currents as to the action of the sun's rays, is shown by the fact that, during the ex-

periments outside on a cloudy day, strong atmospheric currents did not by any means raise the daily quantity to what it was on a calm but clear day. But it must be remembered that currents are much more effectual in hastening the process in clear than in cloudy weather, for the simple reason that the sun's rays opening the pores of the plant, allow of the more ready escape of aqueous vapor.

Of the influence of currents, then, it might be stated, from what has been observed, that in clear weather they are very effectual in favoring the process; in cloudy weather their influence is not so noticeable. On clear days strong currents increased the amount over that of calm days by about one-fifth or even one-fourth.

It was found, in every instance tried, that, other things being considered, the complement of the dew point, or the dryness of the air, modified in a marked degree the rate of transpiration; and this appeared to be, in a measure at least, independent of the temperature, as the latter condition did not seem to affect perceptibly the amount evaporated, unless, as is usually the case, the relative humidity was correspondingly low.

A few calculations may serve to impress the importance of the ratio of transpiration, deduced from these experiments. According to the above rate the Washington Elm, at Cambridge, a tree, it is stated, of no very large size, with its 200,000 square feet of leaf surface, would transpire 7¾ tons of watery vapor in twelve hours (day) of clear weather.

Carrying the calculation further, a grove consisting of five hundred trees, each with a leaf surface equal to that of the elm mentioned, would return to the atmosphere 3906 tons of aqueous vapor in twelve hours. Even supposing this to be much overestimated, it may very fairly be concluded from the facts given that the evaporation of watery vapor from plants is a powerful agent in maintaining the humidity of the surrounding air. And if the above data be correct, a strong argument is furnished in support of the belief that vegetation influences, in a great degree, the rainfall of a region of country.

The practical advantage of keeping plants in occupied rooms, in which the air is generally dryer than outside, has, also, from the results obtained, received further demonstration.